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Correlations for Genetic Expression for Growth of Calves of Hereford and Angus Dams Using a Multivariate Animal Model^{1,2}

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ABSTRACT: The purpose of this study was to estimate the correlation between the expression of genes from sires in purebred and crossbred progeny (r_{PC}) and in Hereford and Angus F_1 calves (r_{HA}). Performance traits were weights at birth, 200 d, and 365 d. Progeny from Hereford, Polled Hereford, and Angus bulls mated to Hereford or Angus cows were used to estimate r_{PC} . Progeny from Charolais, Short-horn, Simmental, Limousin, Maine-Anjou, Chianina, Gelbvieh, Tarentaise, and Salers bulls mated to Hereford or Angus cows were used to estimate r_{HA} . Performances in purebreds (P) and crosses (C) or in Hereford (H) and Angus (A) F_1 calves were treated as separate traits. A multivariate animal model with birth year-cow age-sex subclasses, random correlated direct and maternal additive genetic effects, and maternal permanent environmental effects was used. Separate analyses were done by breed of sire. A derivative-free algorithm was used to obtain REML

estimates of (co)variance components. Weighted averages across breeds of estimates of heritability for P, C, H, and A were, respectively, .61, .51, .47, and .40 for birth weight, .41, .46, .37, and .34 for weaning weight, and .50, .49, .42, and .46 for yearling weight. Estimates of r_{PC} ranged from .88 to .97, .55 to .94, and .68 to .86 for weights at birth, 200 d, and 365 d, respectively. Estimates of r_{HA} ranged from .43 to .99, .56 to .95, and .50 to .98 for weights at birth, 200 d, and 365 d, respectively. Weighted averages of estimates of r_{PC} and r_{HA} across sire breeds were, respectively, .93 and .85 for birth weight, .77 and .73 for weaning weight, and .76 and .86 for yearling weight. These results indicate that ranking of sires producing purebreds or crosses, or crossbred calves from different breeds of dams, is approximately the same for birth and yearling weights, but some reranking might occur for weaning weight.

Key Words: Genetic Correlation, Beef Cattle, Growth

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Introduction

Several reports have shown that selection based on EPD of sires for growth traits has resulted in significant genetic progress in the beef cattle industry (e.g., AAA, 1991; APHA, 1991). Sizable breed differences and heterosis effects for economically important traits have been observed (Long, 1980; Cundiff et al., 1986; Wyatt and Franke, 1986). These findings stimulated studies to use both within- and between-breed genetic variation (Kinghorn, 1982; Elzo and

Famula, 1985; Swan and Kinghorn, 1992). Notter (1989) discussed the possibility of calculating across-breed EPD in beef cattle. One piece of information that is needed is to determine the importance of sire \times breed of dam interaction. If this interaction is important, then the use of models to predict genetic values of sires under a particular maternal environment may be needed (Elzo and Famula, 1985; Swan and Kinghorn, 1992).

Sire \times breed of dam interactions may be due to effects of scale and(or) reranking of breeding values of sires when mated to different breeds of dams. Falconer (1952) pointed out that the importance of genotype \times environment interaction can be estimated with a genetic correlation (i.e., expression of a trait in two environments can be regarded as different traits that are genetically correlated). Thus, a genetic correlation smaller than unity indicates genotype \times environment interaction. Multiple-trait procedures to estimate genetic correlations between traits measured on different animals can be used to quantify the

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degree of reranking of sires' breeding values when mated to different dam breeds, and simultaneously to adjust for effects of scale.

The purpose of this study was to assess the importance of reranking of sires when mated to produce purebred or crossbred calves, as well as to produce F_1 calves from Hereford or Angus dams.

Materials and Methods

Data came from a topcross experiment designed to characterize germplasm from different sire breeds representing diverse biological types when mated to Hereford and Angus cows at the Meat Animal Research Center (MARC) in Clay Center, NE. Although more than 26 sire breeds have been evaluated at MARC, only breeds with current national cattle genetic evaluations were included in this study. Sires of the Hereford, Angus, Polled Hereford, Simmental, Limousin, Charolais, Maine-Anjou, Chianina, Tarentaise, Shorthorn, Gelbvieh, and Salers breeds were mated to Hereford and Angus cows to produce the first generation of the Germplasm Evaluation Program (GPE). Figure 1 shows when the sire breeds were used at MARC. Some reference sires of the Hereford, Angus, and Polled Hereford breeds were used in all time periods (cycles) to provide ties among the data. New samples of Hereford, Angus, Polled Hereford, and Charolais bulls born since 1982 were used in cycle IV of the GPE program. Performance traits studied were birth weight, 200-d weight (weaning weight), and 365-d weight (yearling weight).

Calf performances in each maternal environment (breed of dam) were treated as separate traits. Sire breeds were divided into two groups so that two types of correlations were estimated from within breed of sire analyses. In the first group, Angus, Hereford, and Polled Hereford sire breeds produced purebred and crossbred calves, and so the first type of correlation estimated was between the expression of genes from the sires in purebred or crossbred calves (r_{PC}). Polled Hereford \times Hereford crosses were considered purebreds. The second group included all other sire breeds producing F_1 cross calves from Hereford or Angus dams. Thus, the second type of correlation was between the expression of genes of the sires in crossbred calves out of Hereford or Angus cows (r_{HA}).

Table 1 presents the number of sires, dams, and purebred and crossbred progeny for birth weight, weaning weight, and yearling weight. On average across sire breeds, 13 cows were mated per sire and 15% of the cows had more than one calf. Table 2 presents the number of sires, dams, and crossbred progeny from Hereford and Angus cows for birth weight, weaning weight, and yearling weight. Variation in number of animals existed across sire breeds. Charolais had the largest number of sires (65) and

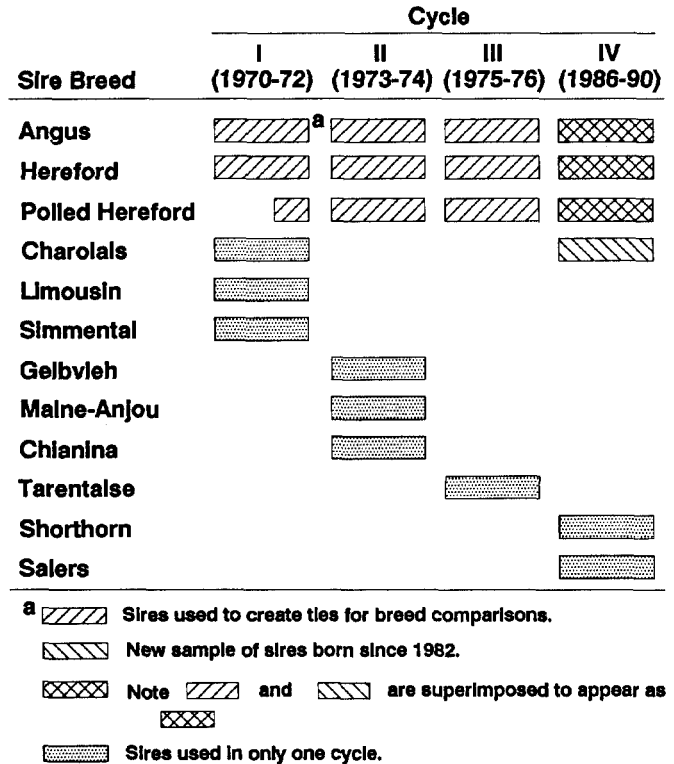


Figure 1. Periods of time when progeny from Hereford or Angus cows were produced out of several sire breeds.

Tarentaise the smallest (7). The number of progeny was largest for Charolais and smallest for Shorthorn. Averaged across sire breeds, 11 cows were mated per sire and 6% of the cows had more than one calf.

Management of these animals has been reported by Smith et al. (1976a,b), Laster et al. (1976, 1979), Gregory et al. (1978, 1979a,b), and Cundiff et al. (1981, 1984). In brief, calves were born in the spring, castrated within 24 h, and weaned at approximately 200 d of age, except that calves born in 1974 were weaned at 167 d of age because of drought conditions. After weaning, heifers were managed to calve first at 2 yr of age and were fed a diet of approximately 50% corn silage and 50% alfalfa or grass haylage, plus protein and mineral supplement. Steers received a high-energy-density diet for approximately 196 d, after a preconditioning period of 25 to 58 d. Averaged across years and feeding periods, the diets contained (DM basis) approximately 12.8% CP, 9.2% digestible protein, and 2.8 Mcal of ME/kg.

The Model

The percentage of cows with more than one calf ranged from 2 to 18% across the different sire breeds. The first attempt to analyze these data fit a model with only direct genetic random effects, besides fixed effects. However, under this model estimates of

Table 1. Number of sires of each sire breed mated to Hereford (HH) and Angus (AA) dams and numbers of purebred (PB) and crossbred (XX) calves with weights at birth (BWT), 200 days (WWT), and 365 days (YWT)

Breed of sire	No. of sires			No. of dams						No. of progeny					
				HH			AA			PB			XX		
	BWT	WWT	YWT	BWT	WWT	YWT	BWT	WWT	YWT	BWT	WWT	YWT	BWT	WWT	YWT
Angus	81	81	81	512	491	465	430	402	392	494	461	446	626	595	551
Hereford	55	54	53	306	284	276	474	456	418	329	302	289	571	540	484
Polled Hereford	22	22	22	99	98	97	201	195	183	103	102	100	210	203	186

additive genetic variances seemed to be biased upward because of covariance among records from the same dam, as discussed by James (1991) for the case of repeated records on the same animal. A second analysis fit both direct genetic and maternal permanent environment effects. Because traits such as birth weight, weaning weight, and even yearling weight of the calf are known to be influenced by the maternal environment, which is due in part to the genetic make up of the cow, a complete model should include, in addition to the previous effects, the genetic maternal effect plus the covariance between direct and maternal genetic effects.

A procedure outlined by James (1991) was extended to attempt to quantify the amount of bias in the estimate of the genetic variance for direct effects when fitting a model with only direct genetic and permanent environmental effects, assuming that the correct model also includes maternal genetic effects (see Appendix). Expectations of variance components based on MINQUE estimators were obtained. After using different combinations of variances due to direct genetic and permanent environmental effects relative to the phenotypic variance as starting values, this procedure suggested for these data that the genetic variance for direct effects would be biased upward by approximately 18% because of the variance of mater-

nal genetic effects and by approximately 15% because of positive covariance between direct and maternal genetic effects. Hence, if the covariance between direct and maternal effects was negative but the same size as the variance for maternal effects, the bias would be nil.

A model including fixed environmental effects plus correlated direct and maternal additive genetic effects and maternal permanent environmental effects was assumed to be appropriate for these data. Because each performance trait was measured on calves of different dam breeds, except for direct and maternal genetic effects, all random effects were assumed to be uncorrelated. The model for traits (e.g., birth weight) expressed in Hereford or Angus maternal environments, **h** or **a**, respectively, can be represented as follows:

$$\begin{aligned} \mathbf{y}_h &= \mathbf{X}_h \mathbf{b}_h + \mathbf{Z}_h \mathbf{g}_h + \mathbf{M}_h \mathbf{m}_h + \mathbf{W}_h \mathbf{p}_h + \mathbf{e}_h \\ \mathbf{y}_a &= \mathbf{X}_a \mathbf{b}_a + \mathbf{Z}_a \mathbf{g}_a + \mathbf{M}_a \mathbf{m}_a + \mathbf{W}_a \mathbf{p}_a + \mathbf{e}_a \end{aligned}$$

where **y** is the vector of observations, **b** is the vector of fixed effects (birth year-cow age-sex subclasses), **X** is the matrix that associates **b** with **y**, **g** is the vector of breeding values for direct genetic effects, **Z** is the matrix that associates **g** with **y**, **m** is the vector of breeding values for maternal genetic effects, **M** is the

Table 2. Number of sires of each sire breed mated to Hereford (HH) and Angus (AA) dams and numbers of Hereford (XH) and Angus (XA) crossbred calves with weights at birth (BWT), 200 days (WWT), and 365 days (YWT)

Breed of sire	No. of sires			No. of dams						No. of progeny					
				HH			AA			XH			XA		
	BWT	WWT	YWT	BWT	WWT	YWT	BWT	WWT	YWT	BWT	WWT	YWT	BWT	WWT	YWT
Charolais	65	64	63	270	240	232	290	257	220	293	257	248	314	276	235
Shorthorn	26	26	26	81	75	75	90	87	85	83	77	77	99	94	92
Simmental	28	27	27	192	167	160	197	181	149	208	180	172	214	197	160
Limousin	20	20	20	193	166	161	175	164	158	206	176	170	182	171	165
Maine-Anjou	18	18	18	96	84	82	112	104	104	100	88	86	118	109	109
Chianina	20	20	20	112	100	100	119	110	110	116	104	104	122	112	112
Gelbvieh	24	24	24	164	150	148	177	166	164	175	160	158	187	173	171
Tarentaise	7	7	7	66	62	61	125	123	119	68	64	63	131	127	123
Salers	27	27	27	76	72	71	100	94	92	80	75	74	108	101	99

matrix that associates \mathbf{m} with \mathbf{y} , \mathbf{p} is the vector of permanent environmental plus nonadditive genetic effects contributed by dams to their progeny, \mathbf{W} is the matrix that associates \mathbf{p} with \mathbf{y} , and \mathbf{e} is the vector of residual effects peculiar to observations that are not explained by other parts of the model. Birth date was included in \mathbf{b} as a covariate for birth weight.

For both traits combined into single vectors and matrices, the multiple-trait animal model can be represented as follows:

$$\begin{bmatrix} \mathbf{y}_h \\ \mathbf{y}_a \end{bmatrix} = \begin{bmatrix} \mathbf{X}_h & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_a \end{bmatrix} \begin{bmatrix} \mathbf{b}_h \\ \mathbf{b}_a \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_h & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_a \end{bmatrix} \begin{bmatrix} \mathbf{g}_h \\ \mathbf{g}_a \end{bmatrix} + \begin{bmatrix} \mathbf{M}_h & \mathbf{0} \\ \mathbf{0} & \mathbf{M}_a \end{bmatrix} \begin{bmatrix} \mathbf{m}_h \\ \mathbf{m}_a \end{bmatrix} + \begin{bmatrix} \mathbf{W}_h & \mathbf{0} \\ \mathbf{0} & \mathbf{W}_a \end{bmatrix} \begin{bmatrix} \mathbf{p}_h \\ \mathbf{p}_a \end{bmatrix} + \begin{bmatrix} \mathbf{e}_h \\ \mathbf{e}_a \end{bmatrix}$$

with

$$\mathbf{E} \begin{bmatrix} \mathbf{y}_h \\ \mathbf{y}_a \end{bmatrix} = \begin{bmatrix} \mathbf{X}_h & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_a \end{bmatrix} \begin{bmatrix} \mathbf{b}_h \\ \mathbf{b}_a \end{bmatrix}$$

and

$$\text{Var} \begin{bmatrix} \mathbf{g}_h \\ \mathbf{g}_a \\ \mathbf{m}_h \\ \mathbf{m}_a \end{bmatrix} = \begin{bmatrix} \sigma_{g_h}^2 \mathbf{A} & \sigma_{g_{ha}} \mathbf{A} & \sigma_{gm_h} \mathbf{A} & \mathbf{0} \\ \sigma_{g_{ha}} \mathbf{A} & \sigma_{g_a}^2 \mathbf{A} & \mathbf{0} & \sigma_{gm_a} \mathbf{A} \\ \sigma_{gm_h} \mathbf{A} & \mathbf{0} & \sigma_{m_h}^2 \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \sigma_{gm_a} \mathbf{A} & \mathbf{0} & \sigma_{m_a}^2 \mathbf{A} \end{bmatrix},$$

$$\begin{bmatrix} \mathbf{Z}_h' \mathbf{r}^{hh} \mathbf{Z}_h + \mathbf{g}^{hh} \mathbf{A}^{-1} & \mathbf{g}^{ha} \mathbf{A}^{-1} \\ \mathbf{g}^{ha} \mathbf{A}^{-1} & \mathbf{Z}_a' \mathbf{r}^{aa} \mathbf{Z}_a + \mathbf{g}^{aa} \mathbf{A}^{-1} \\ \mathbf{M}_h' \mathbf{r}^{hh} \mathbf{Z}_h + \mathbf{gm}^{hh} \mathbf{A}^{-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{M}_a' \mathbf{r}^{aa} \mathbf{Z}_a + \mathbf{gm}^{aa} \mathbf{A}^{-1} \end{bmatrix}$$

$$\text{Var} \begin{bmatrix} \mathbf{p}_h \\ \mathbf{p}_a \end{bmatrix} = \begin{bmatrix} \sigma_{p_h}^2 \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \sigma_{p_a}^2 \mathbf{I} \end{bmatrix},$$

$$\text{Var} \begin{bmatrix} \mathbf{e}_h \\ \mathbf{e}_a \end{bmatrix} = \begin{bmatrix} \sigma_{e_h}^2 \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \sigma_{e_a}^2 \mathbf{I} \end{bmatrix}$$

where \mathbf{A} is the numerator relationship matrix and \mathbf{I} are identity matrices of appropriate order, and the \mathbf{g} , \mathbf{p} , and \mathbf{e} vectors are uncorrelated. The variance-covariance matrix for genetic effects is $\mathbf{G} = \mathbf{G}_0 * \mathbf{A}$, with $\mathbf{G}^{-1} = \mathbf{G}_0^{-1} * \mathbf{A}^{-1}$, and the variance-covariance matrix for residual effects is $\mathbf{R} = \mathbf{R}_0 * \mathbf{I}$, with $\mathbf{R}^{-1} = \mathbf{R}_0^{-1} * \mathbf{I}$, where \mathbf{G}_0^{-1} and \mathbf{R}_0^{-1} are symbolized as follows:

$$\mathbf{G}_0^{-1} = \begin{bmatrix} \mathbf{g}^{hh} & \mathbf{g}^{ha} & \mathbf{gm}^{hh} & \mathbf{0} \\ \mathbf{g}^{ha} & \mathbf{g}^{aa} & \mathbf{0} & \mathbf{gm}^{aa} \\ \mathbf{gm}^{hh} & \mathbf{0} & \mathbf{m}^{hh} & \mathbf{0} \\ \mathbf{0} & \mathbf{gm}^{aa} & \mathbf{0} & \mathbf{m}^{aa} \end{bmatrix},$$

and

$$\mathbf{R}_0^{-1} = \begin{bmatrix} \mathbf{r}^{hh} & \mathbf{0} \\ \mathbf{0} & \mathbf{r}^{aa} \end{bmatrix}.$$

The mixed-model equations can be represented as $\mathbf{C}\hat{\mathbf{s}} = \mathbf{r}$, where \mathbf{C} is the coefficient (left-hand side) matrix, $\hat{\mathbf{s}}$ is the solution vector, and \mathbf{r} is the vector of right-hand sides. The diagonal block of \mathbf{C} associated with direct and maternal genetic effects can be written as follows:

Note that the covariance for direct genetic effects between traits will be estimated based only on the relationships between calves of Hereford and Angus cows.

Estimation of (Co)variance Components

Variance components were estimated by REML procedures. Maximum likelihood estimation consists of obtaining estimates of the parameters (i.e., variance components) that maximize the likelihood function (λ). Maximizing λ is the same as maximizing the $\log \lambda$, or minimizing $-2 \log \lambda$, which can be written as follows:

$$\begin{aligned} & \text{constant} + \log |\mathbf{G}| + \log |\mathbf{S}| + \log |\mathbf{R}| \\ & + \log |\mathbf{C}^\circ| + \mathbf{y}'\mathbf{P}\mathbf{y} \end{aligned}$$

where \mathbf{S} is the variance-covariance matrix for maternal permanent environmental effects, \mathbf{C}° is the full rank coefficient matrix, and $\mathbf{y}'\mathbf{P}\mathbf{y}$ is the generalized residual sum of squares.

Meyer (1991) presented ways to evaluate the likelihood function for the multiple-trait case. Meyer used Gaussian elimination procedures to evaluate simultaneously $\log |\mathbf{C}|$ and $\mathbf{y}'\mathbf{P}\mathbf{y}$, which are the most expensive in terms of computer time. Boldman and

Van Vleck (1991) described the use of a sparse matrix software package, SPARSPAK (George et al., 1980), to evaluate more efficiently these two components. Thus, the evaluation of the likelihood function was done as follows:

$$\begin{aligned}\log|\mathbf{G}| &= \mathbf{NA} \left[\sum_{i=1}^{ng} \text{eigen}(\mathbf{G}_o) \right] + ng \cdot \log|\mathbf{A}|, \\ \log|\mathbf{S}| &= \sum_{i=1}^{nt} \mathbf{NC}_i \cdot \log \sigma_{p_i}^2, \\ \log|\mathbf{R}| &= \sum_{i=1}^{nt} \mathbf{NR}_i \cdot \log \sigma_{e_i}^2\end{aligned}$$

where \mathbf{NA} is the number of animals in the relationship matrix, ng is the order of \mathbf{G}_o , nt is the number of traits, \mathbf{NC}_i is the number of dams for trait i , and \mathbf{NR}_i is the number of records of trait i .

Computation of $\log|\mathbf{C}^\circ|$ and $\mathbf{y}'\mathbf{P}\mathbf{y}$ was based on a Cholesky factorization of the coefficient matrix as follows (Boldman and Van Vleck, 1991). If $\mathbf{C}^\circ = \mathbf{LL}'$, where \mathbf{L} is the Cholesky factor, a lower triangular matrix, then

$$\log|\mathbf{C}^\circ| = \sum_{i=1}^{nc} \log(\mathbf{L}_{ii}^2),$$

and

$$\mathbf{y}'\mathbf{P}\mathbf{y} = \mathbf{y}'\mathbf{R}^{-1}\mathbf{y} - \hat{\mathbf{s}}'\mathbf{r}$$

where nc is the rank of \mathbf{C} , and $\hat{\mathbf{s}}$ is computed by successively solving two triangular systems by forward and backward substitution.

Optimization of the likelihood function was done through direct search, that is, without the use of derivatives, using the downhill simplex algorithm of Nelder and Mead (1965). Iterations were stopped when the variance of function values ($-2 \log \lambda$) of the simplex was less than 1×10^{-9} .

This multiple-trait DFREML program was developed by K. Boldman and D. Van Vleck at the University of Nebraska. This program allows data with missing observations and different models for the various traits.

The same model was used on both types of data sets: 1) purebred and crossbred and 2) Hereford and Angus F_1 crosses.

Results and Discussion

Genetic Parameters for Purebreds and Crosses

Estimates of direct (h^2) and maternal (m^2) heritabilities, of correlations between direct and maternal (r_{GM}) genetic effects, and of ratios of variances of permanent environmental (c^2) effects to the phenotypic variance for different performance traits of purebred and crossbred calves are shown in Table 3.

Meyer (1989) evaluated ways to approximate standard errors of variance components for single-trait models with increasing number of random effects. The approximation was somewhat satisfactory only for the cases of models with direct genetic or direct genetic plus permanent environmental effects. With multiple-trait models, the problem of approximation is even

Table 3. Estimates of the variances relative to the phenotypic variance (σ_T^2) for direct (h^2) and maternal (m^2) genetic effects and permanent environmental (c^2) effects and of correlations between direct and maternal (r_{GM}) genetic effects and of correlations (r_{PC}) between the genetic expression of genes from the sires in purebred (P) and crossbred (C) calves with weights at birth, 200 days, and 365 days by breed of sire

Breed of sire	h_P^2	h_C^2	r_{PC}	m_P^2	m_C^2	$r_{GM}(P)$	$r_{GM}(C)$	c_P^2	c_C^2	$\sigma_T^2(P)$	$\sigma_T^2(C)$
Birth wt											
Angus	.62	.63	.92	.01	.12	-.40	.00	.23	.03	17.4	16.0
Hereford	.60	.41	.97	.17	.17	.22	-.09	.00	.00	21.7	19.1
Polled Hereford	.58	.42	.88	.03	.42	.46	.12	.33	.09	24.8	16.8
Average ^a	.61	.51	.93	.06	.18	-.08	-.01	.15	.02	19.7	17.5
200-d wt											
Angus	.50	.51	.94	.21	.29	.25	.22	.11	.00	463.4	610.8
Hereford	.25	.41	.55	.26	.44	.63	-.38	.00	.05	532.6	472.9
Polled Hereford	.45	.48	.77	.22	.02	.18	.55	.24	.19	667.2	463.3
Average ^a	.41	.46	.77	.22	.30	.38	.03	.08	.04	511.1	531.5
365-d wt											
Angus	.56	.42	.68	.14	.20	.38	.59	.03	.01	1,185.8	1,262.1
Hereford	.47	.59	.86	.17	.19	.12	.50	.26	.00	1,130.1	1,237.6
Polled Hereford	.36	.49	.80	.26	.16	.44	-.44	.02	.18	797.9	726.6
Average ^a	.50	.49	.76	.16	.18	.30	.40	.10	.03	1,279.2	1,136.2

^aWeighted by the number of records in each sire-dam combination.

worse. Consequently, estimates of standard errors for estimates in Table 3 were not computed.

No obvious differences for h^2 between purebreds and crosses were observed across the different performance traits. Average estimates of h^2 for purebreds and crosses across sire breeds were, respectively, .61 and .51 for birth weight, .41 and .46 for 200-d weight, and .50 and .49 for 365-d weight. These estimates are somewhat larger than most previous estimates in the literature (e.g., Koger et al., 1975; Woldehawariat et al., 1977; Meyer et al., 1991). Woldehawariat et al. (1977) reported average heritabilities of .45, .24, and .44 for birth, weaning, and yearling weights, respectively. Larger estimates of h^2 , for Hereford and Angus calves, respectively, were reported for birth weight (.42 and .58) and weaning weight (.63 and .66) by Brown et al. (1990).

Estimates of m^2 , c^2 , and r_{GM} were quite variable across breeds of sires. Although the amount of information available to obtain estimates of maternal and permanent environmental effects was limited, those effects were included in the model to improve estimates of variances and covariances for direct genetic effects. Ignoring maternal effects can substantially inflate estimates of direct heritability (Mrode and Thompson, 1990; Meyer et al., 1991).

Generally, estimates of m^2 were smaller than h^2 for both purebreds and crosses and for each performance trait. Average estimates of m^2 for purebreds and crosses by sire breed were, respectively, .06 and .18 for birth weight, .22 and .30 for 200-d weight, and .16 and .18 for 365-d weight. Larger estimates of heritability for direct than for maternal effects in Hereford and Angus calves have been reported for birth weight by Brown et al. (1990) and Kriese et al. (1991) and also for yearling weight by Meyer et al. (1991).

Estimates of r_{GM} for birth weight of purebred and crossbred calves ranged from $-.40$ to $.46$. Averaged across sire breeds, r_{GM} were $-.08$ and $-.01$ for

purebreds and crosses, respectively. For weight at 200 and 365 d most estimates of r_{GM} were positive. Averaged across sire breeds, estimates of r_{GM} for purebreds and crosses were, respectively, .38 and .03 for 200-d weight and .30 and .40 for 365-d weight. Negative estimates of r_{GM} for growth traits commonly have been reported (Koch, 1972; Brown et al., 1990; Kriese et al., 1991; Meyer et al., 1991), although some reports of positive correlations between direct and maternal genetic effects also exist (Koch, 1972; Meyer et al., 1991).

Estimates of c^2 were generally smaller than those for m^2 . Averaged across sire breeds, estimates of c^2 for purebreds and crosses were, respectively, .15 and .02 for birth weight, .08 and .04 for 200-d weight, and .10 and .03 for 365-d weight.

Correlations Between Purebreds and Crosses. Table 3 also shows estimates of correlations for genetic expression for growth traits in purebred and crossbred (r_{PC}) calves. All correlations were positive and larger than .54. Average (weighted by number of calves) estimates were .93, .77, and .76 for weights at birth and 200 and 365 d, respectively. Correlations between purebreds and crosses usually have been estimated to predict the potential use of selection methods to improve performance of crossbred animals (i.e., reciprocal recurrent selection [Wei and van der Steen, 1991]). In general, if r_{PC} is large and positive, methods using purebred selection are more effective than using reciprocal recurrent selection.

The other use of r_{PC} is as an indicator of sire \times breed of dam interactions, that is, to quantify how well the EPD from purebred data of a bull predicts performance of crossbred calves. The results indicate that ranking of bulls for producing purebred calves is different from that for producing crossbred calves, because the correlations were < 1.0 . The question is, What value of r_{PC} will be of biological and economic importance (i.e., such that effects of reranking of sire's

Table 4. Estimates of the variances relative to the phenotypic variance (σ_T^2) for direct (h^2) and maternal (m^2) genetic effects and permanent environmental (c^2) effects and of correlations between direct and maternal (r_{GM}) genetic effects and of correlations (r_{HA}) between the expression of genes from the sires in Hereford (H) and Angus (A) crossbred calves with birth weight by breed of sire

Breed of sire	h_H^2	h_A^2	r_{HA}	m_H^2	m_A^2	$r_{GM}(H)$	$r_{GM}(A)$	c_H^2	c_A^2	$\sigma_T^2(H)$	$\sigma_T^2(A)$
Charolais	.51	.44	.93	.36	.11	-.13	.36	.04	.33	23.4	23.8
Shorthorn	.40	.39	.38	.19	.04	.53	.81	.06	.16	33.5	23.4
Simmental	.31	.46	.94	.03	.28	-.08	.32	.03	.03	21.9	19.5
Limousin	.54	.44	.83	.32	.29	.34	.44	.00	.02	14.9	16.7
Maine-Anjou	.65	.41	.43	.06	.02	.78	.73	.13	.00	22.8	31.7
Chianina	.54	.45	.99	.09	.36	.06	.09	.07	.05	27.3	31.4
Gelbvieh	.62	.53	.95	.23	.21	.00	-.31	.12	.07	24.2	23.8
Tarentaise	.36	.16	.86	.34	.03	.20	.47	.21	.04	17.7	16.6
Salers	.10	.15	.93	.06	.51	-.01	-.37	.74	.17	22.3	23.4
Average ^a	.47	.40	.85	.20	.19	.12	.27	.10	.11	22.5	22.9

^aWeighted by the number of records in each sire-dam combination.

Table 5. Estimates of the variances relative to the phenotypic variance (σ_T^2) for direct (h^2) and maternal (m^2) genetic effects and permanent environmental (c^2) effects and of correlations between direct and maternal (r_{GM}) genetic effects and of correlations (r_{HA}) between the expression of genes from sires in Hereford (H) and Angus (A) crossbred calves with 200-day weight by breed of sire

Breed of sire	h_H^2	h_A^2	r_{HA}	m_H^2	m_A^2	$r_{GM}(H)$	$r_{GM}(A)$	c_H^2	c_A^2	$\sigma_T^2(H)$	$\sigma_T^2(A)$
Charolais	.33	.18	.54	.34	.15	.30	.54	.01	.02	823.4	540.4
Shorthorn	.31	.36	.95	.41	.02	.24	-.07	.09	.01	657.5	595.3
Simmental	.45	.55	.72	.14	.28	.46	-.59	.14	.37	401.0	448.8
Limousin	.41	.43	.66	.13	.27	.69	.29	.18	.04	609.5	678.4
Maine-Anjou	.42	.36	.56	.13	.15	.43	.51	.02	.20	699.2	575.3
Chianina	.44	.42	.74	.27	.45	.34	.23	.11	.02	577.9	638.3
Gelbvieh	.24	.21	.92	.03	.00	-.38	-.03	.48	.22	714.6	447.2
Tarentaise	.43	.48	.82	.20	.22	.41	.43	.12	.01	710.9	573.8
Salers	.41	.21	.95	.17	.70	.27	.19	.16	.01	787.6	489.6
Average ^a	.37	.34	.73	.19	.22	.30	.17	.14	.11	662.4	546.6

^aWeighted by the number of records in each sire-dam combination.

true breeding values should be considered in genetic evaluations)? Robertson (1959) addressed this question and suggested that correlations $< .8$ would be of biological importance. In this study estimates of rp_C for weaning weight of Hereford (.55) sires and for yearling weight of Angus (.68) were relatively low. The average estimates of rp_C for the performance traits, based on Robertson's previous criterion, suggest that important reranking might occur for weights at 200 and 365 d of purebred and crossbred Hereford and Angus calves.

Genetic Parameters for Hereford and Angus Crosses. Estimates of direct (h^2) and maternal (m^2) heritabilities, of correlations between direct and maternal (r_{GM}) genetic effects, and of ratios of variances of permanent environmental (c^2) effects to the phenotypic variance for birth weight on Hereford and Angus crosses are shown in Table 4. Estimates for 200- and 365-d weights are shown in Tables 5 and 6. Large differences in h^2 were observed for birth and

365-d weights, but these estimates were less variable for weaning weight. For Hereford and Angus crosses, respectively, estimates of h^2 ranged from .10 to .65 and from .15 to .53 for birth weight, from .24 to .45 and from .18 to .55 for weaning weight, and from .15 to .67 and from .17 to .75 for yearling weight. Averaged across sire breeds (weighted by the number of calves), estimates of h^2 for Hereford and Angus crosses were, respectively, .47 and .40 for birth weight, .37 and .34 for weaning weight, and .42 and .46 for yearling weight. The average estimates of h^2 are within the range of values previously reported in the literature (e.g., Woldehawariat et al., 1977; Bertrand and Benyshek, 1987; Mrode and Thompson, 1990).

Averaged across sire breeds, estimates of m^2 for Hereford and Angus crosses were, respectively, .20 and .19 for birth weight, .19 and .22 for 200-d weight, and .15 and .15 for 365-d weight. These estimates were generally smaller than estimates for direct heritability, which agrees with reports of

Table 6. Estimates of the variances relative to the phenotypic variance (σ_T^2) for direct (h^2) and maternal (m^2) genetic effects and permanent environmental (c^2) effects and of correlations between direct and maternal (r_{GM}) genetic effects and of correlations (r_{HA}) between the expression of genes from the sires in Hereford (H) and Angus (A) crossbred calves with 365-day weight by breed of sire

Breed of sire	h_H^2	h_A^2	r_{HA}	m_H^2	m_A^2	$r_{GM}(H)$	$r_{GM}(A)$	c_H^2	c_A^2	$\sigma_T^2(H)$	$\sigma_T^2(A)$
Charolais	.43	.67	.98	.02	.01	.14	.11	.35	.00	1,257.2	1,197.3
Shorthorn	.15	.17	.87	.01	.10	.35	-.37	.60	.08	1,454.8	1,231.1
Simmental	.67	.46	.87	.13	.08	.49	-.04	.00	.19	777.2	1,079.3
Limousin	.38	.30	.90	.13	.21	.15	.41	.45	.00	1,278.4	779.9
Maine-Anjou	.39	.28	.50	.17	.16	.37	.84	.23	.00	963.8	863.4
Chianina	.23	.75	.97	.52	.16	.12	.00	.17	.00	924.9	882.5
Gelbvieh	.51	.65	.92	.23	.46	.34	-.20	.00	.00	1,545.4	1,117.9
Tarentaise	.47	.21	.59	.09	.03	.31	.44	.16	.11	594.0	748.8
Salers	.17	.38	.77	.23	.21	.62	.17	.16	.20	623.5	798.7
Average ^a	.42	.46	.86	.15	.15	.29	.14	.23	.05	1,176.7	988.4

^aWeighted by the number of records in each sire-dam combination.

Bertrand and Benyshek (1987) for Limousin and Brangus calves and Garrick et al. (1989) for Simmental-sired calves. Estimates of r_{GM} were generally positive and averaged across sire breeds for Hereford and Angus crosses were, respectively, .12 and .27 for birth weight, .30 and .17 for 200-d weight, and .29 and .14 for 365-d weight. These results are different from most reports in the literature (Koch, 1972; Bertrand and Benyshek, 1987; Garrick et al., 1989), which have found negative correlations between direct and maternal genetic effects for growth traits.

Variance of permanent environmental effects for Hereford and Angus crosses, respectively, accounted on the average for 10 and 11% of the phenotypic variance for birth weight, 14 and 11% for 200-d weight, and 23 and 5% for 365-d weight.

Correlations Between Hereford and Angus Crosses. Estimates of correlations (r_{HA}) for the genetic expression for growth traits of first-cross calves from various sire breeds mated to Hereford or Angus dams are shown in Tables 4, 5, and 6 for weights at birth, 200 d, and 365 d, respectively. For birth weight all estimates of r_{HA} were $> .80$, except for Shorthorn (.38) and Maine-Anjou (.43) sire breeds. For yearling weight most of the estimates of r_{HA} were $> .80$, except for Maine-Anjou (.50), Tarentaise (.59), and Salers (.77) sire breeds. However, for weaning weight many estimates of r_{HA} were $< .80$ and the average (weighted by the number of calves) across sire breeds was .73. Thus, there is an indication that rankings of sires for weaning weight might change when those sires are used to produce crossbred calves from Hereford or Angus maternal environments.

General. Interest in estimates of correlation between purebred and crossbred progeny, or between crossbred progeny from different breeds of dam, results from interest in taking advantage of both within- and among-breed selection. National cattle evaluations in the beef industry are currently carried out on approximately 18 breeds and are based mainly on purebred data. Several studies have estimated the importance of sire \times breed of mate interactions, either by looking at the significance of the interaction effect from the analysis of variance, or at estimates of correlations between estimated breeding values of sires producing progeny from different dam breeds. Results have been somewhat contradictory. Koger et al. (1975), working with Angus, Hereford, and Brahman cattle, reported that interactions of sire \times breed of dam were not significant, and genetic correlations between purebred and backcross progeny were .95 and 1.07 for birth and 205-d weights. Large correlations between purebred and half-sib Angus, Hereford, and Shorthorn calves were also observed by Dunn et al. (1970) for birth and weaning weights. However, other results have indicated important sire \times breed of dam interactions. Massey and Benyshek (1981) found interactions when Limousin sires were

mated to Hereford and Angus cows to be significant. Correlations between responses in Hereford and Angus crosses were .81, .78, and .62 for weights at birth, 205 d, and 365 d. Also, Tilsch et al. (1989), working with Simmental and Charolais commercial calves, reported that correlations between breeding values of purebreds and crosses were low, ranging from $-.01$ to .46.

All previous studies have assumed equal variances across breeds, which makes it difficult to distinguish how much of the interaction effect is due to changes in rank for a sire's progeny from one breed of dam to another and how much is due to changes in magnitude of sire differences (i.e., heterogeneity of variances). In the present study, variances and covariances were estimated for each breed group and, therefore, potential heterogeneity of variances was taken into account. Thus, estimates of correlations reported here should reflect the magnitude of association of true breeding values of the sires when mated to different breeds of dam. Although large sampling errors are associated with the correlation estimates, because they are based only on relationships between half-sib groups, these results indicate that reranking of sires might occur when these sires are used to produce purebreds and crosses, or crossbred calves from different breeds of dams, particularly for 200-d weight.

Currently, performance records for cattle genetic evaluations in the beef industry are obtained almost entirely in purebred herds. Considering the possible costs involved in obtaining and analyzing records from crossbred cattle, and given that correlations across maternal environments were large and positive, justification for changing genetic evaluation procedures would be difficult.

Procedures to consider sire \times breed of dam interactions in cattle genetic evaluation in the beef industry are complex. Alternative prediction methods have been developed, either using multitrait models (Swan and Kinghorn, 1992) treating performance in each breed of dam as a different trait, as was done in this study, or fitting sire \times breed of dam interaction directly in the model (Elzo and Famula, 1985). As acknowledged by Swan and Meyer (1991), more information about estimates of correlations between purebreds and crosses or between crosses from different dam breeds is required before considering prediction procedures including sire \times breed of dam interactions in the model.

Implications

Progeny data from sires of various breeds mated to different breeds of dams can be used to evaluate the importance of sire \times breed of dam interaction. Results from this study indicate that ranking of sires producing purebreds or crosses, or crossbred calves from

different breeds of dams, is approximately the same for birth and yearling weight, but some reranking might occur for weaning weight. Consideration of these interactions in genetic evaluations allows prediction of breeding values of sires producing progeny under a particular maternal environment.

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APPENDIX

Assume the correct model is

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{Z}_3\mathbf{u}_3 + \mathbf{e}$$

with $\mathbf{E}[\mathbf{y}] = \mathbf{Xb}$, and

$$\begin{aligned} \text{Var}(\mathbf{y}) = & \mathbf{Z}_1\mathbf{A}_1\mathbf{Z}_1'\sigma_1^2 + \mathbf{Z}_2\mathbf{A}_2\mathbf{Z}_2'\sigma_2^2 + (\mathbf{Z}_1\mathbf{A}_{12}\mathbf{Z}_2' \\ & + \mathbf{Z}_2\mathbf{A}_{12}'\mathbf{Z}_1')\sigma_{12} + \mathbf{Z}_3\mathbf{Z}_3'\sigma_3^2 + \mathbf{I}\sigma_0^2 \end{aligned}$$

and that the model used for analysis is

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{Z}_3\mathbf{u}_3 + \mathbf{e}$$

with $\mathbf{E}[\mathbf{y}] = \mathbf{Xb}$, and

$$\text{Var}(\mathbf{y}) = \mathbf{Z}_1\mathbf{A}_1\mathbf{Z}_1'\sigma_1^2 + \mathbf{Z}_3\mathbf{Z}_3'\sigma_3^2 + \mathbf{I}\sigma_0^2$$

where the subscripts indicate direct genetic effects (1), maternal genetic effects (2), permanent environmental effects (3), and residual effects (0).

Sampling theory of REML estimation is not well-developed (James, 1991). However, expectations and variances of quadratic estimators such as MINQUE (Rao, 1972) are simple applications of the rules to obtain means and variances of quadratic forms (Searle, 1982). Iterative MINQUE under normality, if convergence is within the parameter space, equals REML estimators, providing the starting values for both procedures are the same (Searle, 1979). Also, a MINQUE estimator is equal to a first iterate solution of REML. Considering the relationship between REML and MINQUE estimators, the expectation of MINQUE estimators was obtained. Using w_0, w_1 , and

w_3 as weights or "operational values" for σ_0^2, σ_1^2 , and σ_3^2 , respectively, the MINQUE equations are as follows:

$$\begin{bmatrix} T_{11} & T_{13} & T_{10} \\ T_{13} & T_{33} & T_{30} \\ T_{10} & T_{30} & T_{00} \end{bmatrix} \begin{bmatrix} \hat{\sigma}_1^2 \\ \hat{\sigma}_3^2 \\ \hat{\sigma}_0^2 \end{bmatrix} = \begin{bmatrix} q_1 \\ q_3 \\ q_0 \end{bmatrix}$$

or

$$\mathbf{T}\hat{\sigma} = \mathbf{q}$$

where $T_{11} = \text{tr}(\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1')$, $T_{13} = \text{tr}(\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{PZ}_3\mathbf{Z}_3')$, $T_{10} = \text{tr}(\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{P})$, $T_{33} = \text{tr}(\mathbf{PZ}_3\mathbf{Z}_3'\mathbf{PZ}_3\mathbf{Z}_3')$, $T_{30} = \text{tr}(\mathbf{PZ}_3\mathbf{Z}_3'\mathbf{P})$, $T_{00} = \text{tr}(\mathbf{PP})$, $q_1 = \mathbf{y}'\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{Py}$, $q_3 = \mathbf{y}'\mathbf{PZ}_3\mathbf{Z}_3'\mathbf{Py}$, $q_0 = \mathbf{y}'\mathbf{PPy}$, $\mathbf{P} = \mathbf{W}^{-1} - \mathbf{W}^{-1}\mathbf{X}(\mathbf{X}'\mathbf{W}^{-1}\mathbf{X})^{-1}\mathbf{X}'\mathbf{W}^{-1}$, and $\mathbf{W} = \mathbf{Z}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{w}_1 + \mathbf{Z}_3\mathbf{Z}_3'\mathbf{w}_3 + \mathbf{I}w_0$.

Then, estimates of variance components are obtained from

$$\hat{\sigma} = \mathbf{T}^{-1}\mathbf{q}$$

where

$$\mathbf{T}^{-1} = \begin{bmatrix} T_{33}T_{00} - T_{30}T_{30} & T_{10}T_{30} - T_{13}T_{00} & T_{13}T_{30} - T_{10}T_{33} \\ T_{30}T_{10} - T_{13}T_{00} & T_{11}T_{00} - T_{10}T_{10} & T_{10}T_{13} - T_{11}T_{30} \\ T_{13}T_{30} - T_{33}T_{10} & T_{13}T_{10} - T_{11}T_{30} & T_{11}T_{33} - T_{13}T_{13} \end{bmatrix} / D$$

with

$$\begin{aligned} D = & T_{11}T_{33}T_{00} + T_{13}T_{30}T_{10} + T_{10}T_{13}T_{30} - T_{11}T_{30}T_{30} \\ & - T_{13}T_{13}T_{00} - T_{10}T_{10}T_{33}, \end{aligned}$$

Then

$$\mathbf{E}[\hat{\sigma}] = \mathbf{T}^{-1}\mathbf{E}[\mathbf{q}]$$

so that the expectations of the variance component estimates are as follows:

$$\begin{aligned} \mathbf{E}[\hat{\sigma}_1^2] = & \sigma_1^2 + [(T_{00}T_{33} - T_{30}T_{30}) \text{tr}(\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{PZ}_2\mathbf{A}_2\mathbf{Z}_2')] \sigma_2^2/D \\ & + [(T_{10}T_{30} - T_{13}T_{00}) \text{tr}(\mathbf{PZ}_3\mathbf{Z}_3'\mathbf{PZ}_2\mathbf{A}_2\mathbf{Z}_2')] \sigma_2^2/D \\ & + [(T_{13}T_{30} - T_{10}T_{33}) \text{tr}(\mathbf{PPZ}_2\mathbf{A}_2\mathbf{Z}_2')] \sigma_2^2/D \\ & + [(T_{00}T_{33} - T_{30}T_{30}) 2\text{tr}(\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{PZ}_1\mathbf{A}_{12}\mathbf{Z}_2')] \sigma_{12}/D \\ & + [(T_{10}T_{30} - T_{13}T_{00}) 2\text{tr}(\mathbf{PZ}_3\mathbf{Z}_3'\mathbf{PZ}_1\mathbf{A}_{12}\mathbf{Z}_2')] \sigma_{12}/D \\ & + [(T_{13}T_{30} - T_{10}T_{33}) 2\text{tr}(\mathbf{PPZ}_1\mathbf{A}_{12}\mathbf{Z}_2')] \sigma_{12}/D \\ \mathbf{E}[\hat{\sigma}_3^2] = & \sigma_3^2 + [(T_{30}T_{10} - T_{13}T_{00}) \text{tr}(\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{PZ}_2\mathbf{A}_2\mathbf{Z}_2')] \sigma_2^2/D \\ & + [(T_{11}T_{00} - T_{10}T_{10}) \text{tr}(\mathbf{PZ}_3\mathbf{Z}_3'\mathbf{PZ}_2\mathbf{A}_2\mathbf{Z}_2')] \sigma_2^2/D \\ & + [(T_{10}T_{13} - T_{11}T_{30}) \text{tr}(\mathbf{PPZ}_2\mathbf{A}_2\mathbf{Z}_2')] \sigma_2^2/D \\ & + [(T_{30}T_{10} - T_{13}T_{00}) 2\text{tr}(\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{PZ}_1\mathbf{A}_{12}\mathbf{Z}_2')] \sigma_{12}/D \\ & + [(T_{11}T_{00} - T_{10}T_{10}) 2\text{tr}(\mathbf{PZ}_3\mathbf{Z}_3'\mathbf{PZ}_1\mathbf{A}_{12}\mathbf{Z}_2')] \sigma_{12}/D \\ & + [(T_{10}T_{13} - T_{11}T_{30}) 2\text{tr}(\mathbf{PPZ}_1\mathbf{A}_{12}\mathbf{Z}_2')] \sigma_{12}/D \end{aligned}$$

$$\begin{aligned}
E[\hat{\sigma}_0^2] = & \sigma_0^2 + [(T_{13}T_{30} - T_{33}T_{10}) \text{tr}(\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{PZ}_2\mathbf{A}_2\mathbf{Z}_2')] \sigma_2^2/D \\
& + [(T_{13}T_{10} - T_{11}T_{30}) \text{tr}(\mathbf{PZ}_3\mathbf{Z}_3'\mathbf{PZ}_2\mathbf{A}_2\mathbf{Z}_2')] \sigma_2^2/D \\
& + [(T_{11}T_{33} - T_{13}T_{13}) \text{tr}(\mathbf{PPZ}_2\mathbf{A}_2\mathbf{Z}_2')] \sigma_2^2/D \\
& + [(T_{13}T_{30} - T_{33}T_{10}) 2\text{tr}(\mathbf{PZ}_1\mathbf{A}_1\mathbf{Z}_1'\mathbf{PZ}_1\mathbf{A}_{12}\mathbf{Z}_2')] \sigma_{12}/D \\
& + [(T_{13}T_{10} - T_{11}T_{30}) 2\text{tr}(\mathbf{PZ}_3\mathbf{Z}_3'\mathbf{PZ}_1\mathbf{A}_{12}\mathbf{Z}_2')] \sigma_{12}/D \\
& + [(T_{11}T_{33} - T_{13}T_{13}) 2\text{tr}(\mathbf{PPZ}_1\mathbf{A}_{12}\mathbf{Z}_2')] \sigma_{12}/D
\end{aligned}$$

Because $\mathbf{Z}_1 = \mathbf{I}$, $\mathbf{Z}_2 = \mathbf{Z}_3$, and if dams are unrelated ($\mathbf{A}_2 = \mathbf{I}$), the estimated variances of maternal genetic effects (σ_2^2) will be completely confounded with the variance of permanent environmental effects (σ_3^2).

The degree of confounding of the covariance between direct and maternal genetic effects (σ_{12}) with the different variance component estimates will depend on the degree of relationships between calves and cows (\mathbf{A}_{12}).